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Paleoecology and paleobiogeography of fossil mollusks from Isla Isabela (Galápagos, Ecuador)

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Abstract

Sandy sediments outcropping near Villamil (Isla Isabela, Galápagos) have yielded a fossil molluscan assemblage represented by 42 taxa (23 bivalves and 19 gastropods) and dominated by the lucinids *Divalinga eburea* and *Pegophysema spherica*. The paleocommunity developed on a inner subtidal sandy bottom no deeper than 30–40 m and located near reef habitats; the clear predominance of suspension over deposit feeders is in accordance with the sandy substrate, limiting the organic matter preservation in the seafloor. Although the presence of the fossil bivalve *P. spherica* might indicate a Pliocene age, the modern structure of the fauna and scant radiometric ages proposed to date seem to suggest a Pleistocene age. A biogeographic analysis highlights a large predominance of the Panamic component; the remaining mollusks include a significant endemic component and negligible percentages of forms from neighboring bioprovinces. Other than some differences in percentages, a similar biogeographic pattern results for the other fossil molluscan communities and the modern one of the archipelago. From a taxonomic point of view, most of the fossil and modern assemblages show a high ratio of gastropods to bivalves, whereas in the fauna discussed herein, bivalves are slightly predominant over gastropods.

Keywords: Mollusks; Galápagos Archipelago; Paleoecology; Paleobiogeography

1. Introduction

The Colon Archipelago, better known as the Galápagos Archipelago, is composed of 19 major islands (among which Isabela, Santa Cruz, Fernandina, Santiago, and San Cristobal are the largest) and approximately 50 lesser islands and rocks. The Galápagos straddle the equator about 1000 km west of Ecuador and represent the largest group of oceanic islands in the eastern Pacific.

The geologic history of the archipelago is dominated by volcanic activity that produced lava flows with only a small proportion of fragmental deposits. Nevertheless, scattered marine deposits, some bearing fossil remains, occur on the islands, some of which provide evidence for interpretation of the age of the Galápagos.

In 1991, our research group organized an expedition to the Galápagos Islands to collect both paleontological and stratigraphical data to compare with those data from mainland Ecuador. The main goal was to gain an improved understanding of the taxonomy and paleoecology of the fossil marine faunas of the archipelago and evaluate their paleobiogeographic relationships with the Panamic and neighboring provinces. Although a portion of these data was recently published (Bianucci et al., 1993, 1997a), the chance to examine the large collections of fossil and recent mollusks of Galápagos and mainland Ecuador deposited at the California Academy of Sciences (CAS) and the Academy of Natural Sciences of Philadelphia (ANSP) enabled us to revise the fossil fauna collected at Villamil (Isabela). In this paper, in addition to discussing the paleoecological meaning and possible age of this assemblage, we focus on the biogeographic affinities of the different faunal components and their comparison with other molluscan fossil communities from the Galápagos.

2. Previous investigations

The fossiliferous deposits of the Galápagos were discovered by Charles Darwin in 1835. He noted the presence of molluscan shells in two tuff levels on San

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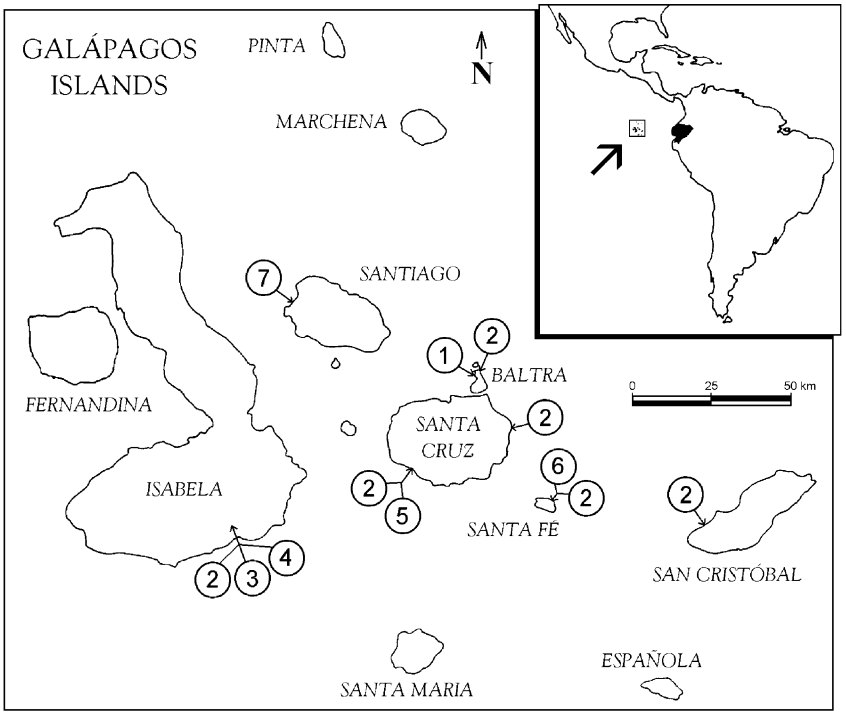

Fig. 1. Map of the Galápagos Islands showing locations of fossiliferous levels considered in this paper, 1 = Hertlein (1972); 2 = Garcia-Talavera (1993); 3 = this paper; 4 = Walker (1991); 5 = Pitt at al. (1986); 6 = Walker (1995); and 7 = Hertlein and Strong (1931).

Cristobal Island. Sixty years later, Wolf (1895) mentioned fossil remains in the palagonite tuff at a height of 100 m a.s.l., without indications of the specific location of these deposits. During a scientific expedition (1905–1906) of the CAS, Ochsner discovered some fossiliferous levels in Baltra, Isabela, and Santa Cruz Islands, as briefly described by Dall (1924). The fossil specimens collected in the 1905–1906 and 1931–1932 expeditions of the CAS were investigated essentially by Dall and Ochsner (1928), Hertlein and Strong (1939) and Hertlein (1972). The paleontological expedition organized by Pitt in 1982 (Lipps and Hickman, 1982; Pitt and James, 1983) visited eight main islands (including Isabela, Santa Cruz, and Santa Fe) and collected fossil mollusks from many marine deposits, but only a portion of these fossils has received attention so far (Nesbitt and Pitt, 1986; Pitt et al., 1986; Walker, 1991, 1995). Finally, Garcia-Talavera (1993) dealt with mollusk remains collected in eight localities on Baltra, Isabela, San Cristobal, Santa Cruz, Santa Fe, and Seymour Islands (Fig. 1).

Most of these papers pertain to systematic analyses, and only a few document paleoecological and taphonomic evidence. Biogeographic observations are chiefly related to individual faunas, and an updated setting for fossil faunas as a whole is lacking.

3. The fossil assemblage of Villamil

The fossil assemblage was recovered from a fossiliferous level exposed at a landing strip-cut, 10–12 m above sea level, near the village of Puerto Villamil (Isabela). Villamil fossils have been investigated chiefly by Dall and Ochsner (1928), Walker (1991), Garcia-Talavera (1993) and Bianucci et al. (1997a), but it is difficult to establish the exact relationships among the fossiliferous localities cited in these papers because of a lack of detailed topographical maps. We believe that our chosen locality (Bianucci et al., 1997a) is equivalent to the Brattle outcrop of Garcia-Talavera (1993).

The stratigraphical sequence investigated (3 m in thickness) is dominated by whitish, coarse, organogenic sands. Only rare relics of curve lamination surfaces at low angles (hummocky bedding) are present due to strong bioturbation. In the upper part of the sequence, poor to moderate bioturbation makes it possible to note a parallel lamination that changes upward to cross- (ripple) and wedge-lamination. The top of the succession is represented by bioclastic marine conglomerates approximately 30 cm thick.

The fossil fauna was collected in the sandy portion just below the laminated levels. The mollusks were collected by hand picking because the cohesive substrate does not allow a bulk sampling. In the rest of the section, fossil remains are very rare, mainly fragmented, and badly preserved.

The presence of these sedimentary structures and coarser sediments in the upper part is linked to a shoaling that might reflect changes in the sea level or local tectonic movements. Taking into account the general tectonic setting of the Galápagos, the second hypothesis seems most reasonable, but the reduced thickness of the outcrop, along with the lack of lateral continuity, do not allow for more precise observations.

Table 1
Taxonomic composition, autoecology, and geographic distribution of fossil mollusks from Isabela

Taxa	SP.	Feeding type	Depth range	Geographical range
Bivalvia				
Anomia peruviana d'Orbigny	1	Suspension	Up to 130 m in depth	G. Calif. ⇑ Perù (Paita); Clipp., Galáp
Arcopsis solida (Sowerby)	9	Suspension	Intertidal	B. Calif. ⇑ Perù (Paita); Galáp
Barbatia reeveana (d'Orbigny)	13	Suspension	Up to 120 m in depth	B. Calif. ⇑ Perù (Zorritos); Clipp., Galáp
B. rostae Berry	9	Suspension	Up to 5 m in depth	B. Calif. ⇑ Ecuador; Galáp
Basterotia peninsulare (Jordan)	3	Suspension	Up to 46 m in depth	B. Calif. ⇑ Ecuador; Galáp
B. quadrata (Hanley)	2	Suspension	From 6 to 120 m	B. Calif. ⇑ Ecuador; Galáp Caribb., Atlan. NW
Chione compta (Broderip)	1	Suspension	From 20 to 30 m	G. Calif. ⇑ Perù (Bayovar); Galáp
Chlamys lowei (Hertlein)	1	Suspension	Up to 146 m in depth	G. Calif. ⇑ Ecuador; Galáp
Ctena galapagana (Dall)	4	Suspension	Up to 40 m in depth	Nicaragua ⇑ Ecuador; Galáp
Diplodonta subquadrata (Carpenter)	1	Suspension	Up to 140 m in depth	B. Calif. ⇑ Galáp
Divalinga eburnea (Reeve)	134	Suspension	Up to 55 m in depth	B. Calif. ⇑ Perù; Galáp
Glycymeris maculata (Broderip)	2	Suspension	From 5 to 45 m	B. Calif. ⇑ Perù (Zorritos); Galáp
Laevicardium elenense (Sowerby)	4	Suspension	Up to 90 m in depth	B. Calif. ⇑ Perù (Zorritos); Galáp
Larkinia multicostata (Sowerby)	1	Suspension	Up to 130 m in depth	B. Calif. ⇑ Panama; Galáp
Lima pacifica d'Orbigny	1	Suspension	Up to 2 m in depth	G. Calif. ⇑ Perù; Galáp
Modiolus capax (Conrad)	1	Suspension	Up to 50 m in depth	G. Calif. ⇑ Perù (Paita); Galáp
Undulostrea megodon Hanley	1	Suspension	Up to 110 m in depth	B. Calif. ⇑ Perù (Paita); Galáp
Papyridea mantaensis Olsson	11	Suspension	From 50 to 120 m	Mexico ⇑ Perù (Zorritos); Galáp
Pegophysema spherica[a] (Dall and Och.)	71	Suspension	From 35 to 170 m[b]	Ecuador; Galáp
Tellina mantaensis Pilsbry and Olsson	2	Deposit	Intertidal	Panama ⇑ Perù (C. la Cruz); Galáp
T. pacifica Dall	5	Deposit	From 5 to 35 m	G. Calif. ⇑ Panama; Galáp
T. reclusa Dall	2	Deposit	From 5 to 70 m	B. Calif. ⇑ Panama; Galáp
Tellina sp.	5	Deposit		
Gastropoda				
Capulus sericeus Burch	1	Parasitic	Up to 180 m in depth	G. Calif.; Mexico, Ecuador; Galáp
Columbella castanea Sowerby	1	Carnivore	Up to 100 m in depth	Galápagos; Panamic
C. fuscata Sowerby	1	Carnivore	Shallow waters	B. Calif. ⇑ Perù; Galáp
Coralliophila sp.	1	Carnivore		
Crepidula aculeata (Gmelin)	11	Suspension	Intertidal	G. Calif. ⇑ Cile; Galáp; Caribb.; W. Pacif.
Diodora alta Adams	4	Herbivore	Up to 30 m in depth	G. Calif. ⇑ Perù N; Galáp
Epitonium minuticosta (Carpenter)	1	Carnivore	From 18 to 140 m	B. Calif. ⇑ Mexico; Galáp
Epitonium sp.	3	Carnivore		
Nassarius caelolineatus Nesb. And Pitt	9	Carnivore	Up to 70 m in depth	Galápagos
N. versicolor (Adams)	2	Carnivore	Up to 46 m in depth	B. Calif. ⇑ Perù; Galáp
Olivella gracilis (Brod. and Sowerby)	3	Carnivore	Shallow waters	Mexico ⇑ Panama; Galáp
Olivella sp.	24	Carnivore		
Pteropoda indet.	–			
Strombina lanceolata (Sowerby)	20	Carnivore	From 4 to 180 m	Ecuador ⇑ Perù; Galáp
Subcancilla cf. *erythrogramma* (Toml.)	1	Carnivore	From 18 to 37 m	B. Calif. ⇑ Colombia; Galáp
Subcancilla sp.	1	Carnivore		
Terebra albemarlensis[a](Dall and Ochs.)	1	Carnivore	Offshore	Galápagos
T. frigata Hinds	21	Carnivore	From 4 to 82 m	Galápagos; Panamic
Trivia fusca (Sowerby)	2	Carnivore	Shallow waters	?Panama ⇑ ?Ecuador; Galáp

SP.: number of specimens, G. Calif.: Gulf of California, B. Calif.: Baja California, Clipp.: Clipperton Islands, Galap.: Galápagos Islands, Caribb. = Caribbean, and W. Pacific = Western Pacific.

[a] Extinct taxa.

[b] Data from the closely related modern species *P. edentuloides.*

Walker (1991) and Garcia-Talavera (1993) inferred similar fates for Urvina Bay and Villamil deposits with regard to rapid tectonic uplift. In any case, the sedimentary features of the deposits overlying the fossiliferous level seem inconsistent with an abrupt tectonic uplift of the sea floor above the sea level in the manner inferred for the Urvina Bay coral community (Malmquist, 1991).

The faunal assemblage is composed mainly of bivalves and gastropods but also includes arthropod pincers, siliceous sponges (spicules), sea urchin spines (*Eucidaris* sp.), barnacle plates, rare foraminifers (including *Cibicides*, *Elphidium*, *Nonion*, *Quinqueloculina*, *Spiroloculina*, *Globigerina*, and *Globigerinoides*), and abraded fragments of corals and briozoa. The examination of specimens from the collections of CAS and ANSP enables us to review the faunal list previously published (Bianucci et al., 1997a).

The mollusk fauna, represented by 42 taxa, among which 23 are bivalves and 19 are gastropods (Table 1), is

dominated by the lucinids *Divalinga eburnea* and *Pegophysema spherica*, though *Terebra frigata* and *Strombina lanceolata* are the most abundant gastropods. The remaining taxa are represented by very few specimens. The abundance of taxa (number of specimens per taxon) was determined following the method suggested by Di Geronimo and Robba (1976), and it is shown in Table 1.

Almost all faunal components were identified at the species level using the most extensive accounts on Pliocene to Recent Panamic and Galápagos megafaunas. Information on species autoecology was obtained from the literature with regard to extant taxa and deduced mainly from closely related modern species or recurrent associations with other species with regard to extinct taxa. Reference was chiefly made to Bernard (1983), Bratcher and Burch (1971), Coan (1999), Keen (1971), Finet (1994a,b 1995), Nesbitt and Pitt (1986), Olsson (1961), Piazza and Robba (1994, 1998), Pitt et al. (1986), Taviani (1979) and Walker (1991, 1995).

4. Paleoecological remarks

The skeletal elements of the fossiliferous level consist of disarticulated and well-preserved shells that are rarely broken and little abraded and have inconspicuous signs of bioerosion and encrustation. Among bivalves, only five specimens of *Divalinga eburnea* and one of *Ctena galapagana* have been identified with conjoined valves but not in life position.

Because most shells represent the deep infaunal lucinids *D. eburnea* and *Pegophysema spherica*, these taphonomic features may be related to a brief reworking event followed by a rapid final burial. Inconspicuous signs of sorting and the lack of shells with a preferential orientation lead us to exclude a significative transport phase. These features may indicate a storm-influenced deposit.

From a trophic standpoint, the suspension feeders (20 taxa, almost all bivalves) display greater diversity than do the carnivorous ones (15 taxa among gastropods), and the difference increases in terms of the number of individuals. The presence of corallivore forms among both carnivorous gastropods (*Coralliophila* sp., epitonids) and echinoids (*Eucidaris* sp.) is noteworthy. Other groups display very low diversity and abundance and constitute a factor of little importance in the trophic structure (4 taxa for detritus feeders, 1 taxa each for herbivores and parasites).

A precise paleodepth inference from the fossil fauna is difficult, mainly because of the very scarce data about the extinct lucinid *P. spherica*, one of the most abundant species of the assemblage. However, taking into account the depth range of its modern counterpart *P. edentuloides* and the bathymetric interval of some fossil assemblages containing *P. spherica* (Hertlein, 1972; Bianucci et al., 1997b), it seems consistent for this taxon to have lived in the moderately shallow environments of the continental shelf. In this case, a comparison with the depth ranges of the rest of the fauna (Table 1) leads us to regard the paleocommunity as indicative of an inner subtidal setting no deeper than 30–40 m. This inference is in agreement with the foraminifer assemblage mentioned previously, the bathymetric range of scattered coral reefs living in the archipelago (Glynn and Wellington, 1983), the sedimentary structures recognized in the depositional sequence, and the taphnomic features.

The presence of few specimens from taxa linked to very shallow waters, such as the intertidal *Arcopsis solida*, *Tellina mantaensis*, and *Crepidula aculeata*, may be related to *postmortem* displacement from their habitats. Moreover, the fossil molluscan communities of the Galápagos Islands that are regarded as intertidal (Walker, 1991, 1995; Garcia-Talavera, 1993) highlight a very different taxonomic composition than that showed in Table 1.

The occurrence of coral fragments, corallivore forms, and coral reef-associated mollusks (*Nassarius caeolineatus* and terebrids) suggests a subtidal situation in sediments that surrounded reef habitats in the original community. The clear predominance of suspension over deposit feeders is in accordance with the sandy grain size of the substrate limiting the organic matter deposition on the seafloor (Sanders, 1958; Di Geronimo et al., 1982), and the high species diversity of predatory gastropods may be due to the abundance of their potential prey among both suspension feeder bivalves and other soft-bodied taxa (e.g. ascidians) (Pavia et al., 1989; Ragaini and Mariani, 1992).

Because the carbon and oxygen isotope composition of mollusk shells represents a potential source of paleoecological and paleoclimatic information, we attempted to analyze several specimens from two species of bivalves (*D. eburnea* and *P. spherica*) and two of gastropods (*Strombina lanceolata* and *Terebra frigata*). Unfortunately, X-ray powder tests evidenced calcitization, varying from 5 to 100%, which makes such a test impossible.

5. Chronostratigraphic setting

The terebrid *Terebra albemarlensis* and the lucinid *Pegophysema spherica*, both erected by Dall and Ochsner (1928), are the only extinct species and represent a small percentage (5.5%) of the assemblage. The former is endemic to Isabela Island, whereas the latter has been recognized in several Pliocene or Plio-Pleistocene deposits of the Galápagos (Hertlein, 1972; Hickman and Lipps, 1985; Garcia-Talavera, 1993; Bianucci et al., 1997a) and in Pliocene of mainland Ecuador (Pilsbry and Olsson, 1941; Bianucci et al., 1997b). This evidence would lead us to refer this fauna to the Pliocene, but the taxonomic composition of the association points to a more recent age (i.e. Pleistocene).

Taking into account the marine fossil faunas of the Galápagos attributed to Pliocene or Plio-Pleistocene, the extinct portion appears quite variable. The assemblages of Baltra contain 7.8 and 28.6% extinct taxa (Hertlein, 1972; Garcia-Talavera, 1993, respectively), and Santa Cruz

(Pitt et al., 1986) provides a value of 10%. The Villamil fossils attain lower percentages: the megagastropod association studied by Walker (1991) provides a value of 4.8%, and Garcia-Talavera (1993) did not even recognize extinct taxa.

The literature provides different radiometric ages for Villamil deposits using the dating of the Sierra Negra and Cape Berkeley volcanoes (0.5 and 0.72 Ma, respectively). Other lava flows outcropping near Villamil appear to be younger (0.15 Ma) (Walker, 1991). In any case, field data do not allow for the evaluation of the stratigraphic relationships among these dated volcanic sediments and the sequence described herein.

In conclusion, though the occurrence of *P. spherica* gives the appearance of a Pliocene age, the very low percentage of extinct taxa (5.5%) and the taxonomic composition of the assemblage seem to suggest a Pleistocene age, an inference that is consistent with the scanty radiometric data previously obtained. In this case, it may be argued that *P. spherica*-survived into the Pleistocene as an endemic species in the Galápagos Islands.

6. Paleobiogeographic setting

As was noted in the first extensive treatments (e.g. Dall and Ochsner, 1928; Hertlein and Strong, 1939) and generally confirmed by followers (e.g. Hertlein, 1972; James and Pitt, 1984; Wellington, 1984), the fossil near shore mollusks of the Galápagos Islands are dominated by Panamic forms.

The fossil association investigated herein supports this view, because the Panamic species largely outnumber (88.9%) the remaining components. However, within the Panamic component, it is possible to distinguish some groups with different biogeographic affinities:

- Taxa limited to the northern and central part, from the Gulf of California to Central America (8.3%);
- Typically Panamic species occurring in the bioprovince as a whole (58.3%); and
- Taxa known to occur in the central and southern part, from Central America to North Peru (22.3%).

The endemic group consists of two gastropod species (*Nassarius caelolineatus* and *T. albemarlensis*) that attain only 5.5%. Negligible percentages (2.8%) are related to Amphiamerican (species that occur in both the Panamic and Caribbean regions) and tropical wide ranging (TWR) components, both represented only by one species (*Basterotia quadrata* and *Crepidula aculeata*, respectively).

Other than some differences in percentages, this biogeographic structure is similar to that described for the recent mollusks of the archipelago (Kay, 1991; Finet, 1995; Kaiser, 1997). The strong predominance of the Panamic taxa appears to be consistent with the modern pattern of the water circulation in both the Panamic and Caribbean Provinces (Finet, 1991), which represents the primary mechanism for dispersal of benthic invertebrates. The considerable percentages of the latter two groups (58.3 and 22.3%, respectively) are consistent with the current that originates in the Gulf of Panama, where a strong upwelling is located, and flows west. The sporadic elements belonging to the first group (8.3%) might be related to the minimal role played by the California Current (CC) and the North Equatorial Countercurrent (NECC) in direct transport of mollusk larvae to Galápagos.

The negligible percentage (2.8%) of Amphiamerican and TWR taxa is chiefly linked to two main physical barriers that affected the faunal exchanges with the Caraibic and Indo-Pacific Bioprovinces: the Central American isthmus (CAI) and Ekman's East Pacific barrier, respectively.

The negligible percentage of Caribbean species in the fossil and modern mollusk assemblages of Galápagos is consistent with the geologic evolution of the CAI (Duque-Caro, 1990; Collins et al., 1996; Cronin and Dowsett, 1996; Haug and Tiedemann, 1998). With regard to the fossil fauna of Isabela, only two species (the Amphiamerican *B. quadrata* and the TWR *C. aculeata*) are present on both sides of the isthmus, whereas five (13.5%) are closely related to corresponding species in the Atlantic (cognate species) (Table 2).

Table 2
Atlantic 'Cognate species' present in the Isabela assemblage

Isabela (Galápagos)	Atlantic
Arcopsis solida	*Arcopsis adamsi*
Ctena galapagana	*Ctena orbiculata*
Divalinga eburnea	*Divalinga quadrisulcata*
Tellina pacifica	*Tellina americana*
Tellina reclusa	*Tellina aequistriata*

The Ekman's East Pacific barrier is a huge marine expanse (approximately 5000 km wide) that runs off the coasts of North, Central, and South America from Canada to Chile and is devoid of oceanic islands. This broad marine barrier separates the offshore islands of the Panamic Province from the eastern archipelagos of the Indo-Pacific and greatly reduces the possibility of west–east faunal exchanges (Grig and Hey, 1992). Therefore, it is not unexpected that the Indo-Pacific representation in modern and fossil mollusks of the Galápagos is very scarce. This component is lacking in our fossil assemblage, where only the TWR species *C. aculeata* appears for both Indo-Pacific and Panamic Provinces.

A temperature and current pattern more favorable to tropical species that acts during the El Niño phenomenon justifies the sporadic appearance of new Indo-Pacific species in the Galápagos (Kay, 1991). Immigrating larvae may be able to settle during these events of warm water conditions, but they are unable to successfully reproduce when the

Table 3
Biogeographic comparison among fossil molluscan assemblages from Galapagos Islands (a = abundance, d = dominance)

		Pliocene		Plio-Pleistocene				Pleistocene														Holocene	
		Baltra 1		Santa Cruz 1		Baltra 2		Isabela 1		San Cristo-bal		Santa Cruz 2		Santa Fé 1		Santa Fé 2		San Salva-dor		This paper		Isabela 2	
		a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d	a	d
Panamic	Gast.	51	53.1%	16	94.1%	13	46.4	17	81%	29	74.4%	9	47.4%	17	56.7%	17	89.5%	55	60.4%	1	–	16	55.2%
	Biv.	22	22.9%	–	–	5	17.8%	–	–	3	7.7%	6	31.6%	6	20%	–	–	14	15.4%	21	–	7	24.1%
Endemic	Gast.	17	17.7%	1	5.9%	8	28.6	2	9.5%	5	12.8%	4	21%	4	13.3%	2	10.5%	11	12.1%	–	5.5%	4	13.8%
	Biv.	3	3.1%	–	–	2	7%	–	–	–	–	–	–	–	–	–	–	3	3.3%	–	–	–	–
Pan./Peruv.	Gast.	1	1%	–	–	–	–	1	4.8%	2	5.1%	–	–	2	6.7%	–	–	2	2.2%	–	–	–	–
	Biv.	–	–	–	–	–	–	–	–	–	–	–	–	1	3.3%	–	–	1	1.1%	–	–	–	–
Peruvian	Gast.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Biv.	1	1%	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1.1%	–	–	–	–
Anfiamer.	Gast.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3.4%
	Biv.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1.1%	1	2.8%	–	–
Pan./Indop.	Gast.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1.1%	–	–	–	–
	Biv.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calif.	Gast.	1	1%	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Biv.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TWR	Gast.	–	–	–	–	–	–	1	4.8%	–	–	–	–	–	–	–	–	1	1.1%	1	2.8%	1	3.4%
	Biv.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Data sources: Baltra 1 Hertlein (1972); Santa Cruz 1 Pitt et al. (1986); Baltra 2, San Cristobal, Santa Cruz 2, Santa Fé 1, and Isabela 2 Garcia-Talavera (1993); Isabela 1* Walker (1991); Santa Fé 2* Walker (1995); and San Salvador Hertlein and Strong (1939).
Only gastropods.

Table 4
Endemic taxa in fossil and recent mollusks of the Galápagos

	Pliocene	Plio-Pleist.	Pleist.	Recent[a]
Gast.	18	26	33	123
Biv.	3	3	4	11
Total	21	29	37	134

[a] Data from Finet (1995).

normal cooler conditions are restablished. However, the El Niño episodes may cause the extinction of some taxa better adapted to cool conditions (Coan, 1988; Kay, 1991). Wellington (1984) and Kay (1991) argue that evidence for immigration and extinction also rises from the fossil record, in that some taxa, such as *Pegophysema sphaerica* and *T. albemarlensis*, that were quite abundant in Pleistocene (?) assemblages became extinct.

7. Biogeographic comparison among molluscan fossil assemblages of the Galápagos

An interpretation of the biogeographic similarities and differences among different molluscan fossil assemblages from the archipelago is lacking in the literature. Therefore, we examined the faunas collected and investigated on the following islands:

Isla Baltra	Hertlein (1972) and Garcia-Talavera (1993)
Isla Isabela	Walker (1991) and Garcia-Talavera (1993); this paper
Isla San Cristobal	Garcia-Talavera (1993)
Isla Santa Cruz	Pitt et al. (1986) and Garcia-Talavera (1993)
Isla Santa Fe	Garcia-Talavera (1993) and Walker (1995)
Isla San Salvador	Hertlein and Strong (1939)

Generally, the Panamic forms are dominant in all assemblages, and the endemic group is decidedly subordinate. The remaining mollusks are divided among components related to neighboring biogeographic regions, but their percentages are negligible (Table 3) (these data are based on taxa at specific levels because distributional ranges at the generic level are not significant for mollusks). The biogeographic mosaic shown in Table 3 is very similar to that for the modern assemblage (Finet, 1991, 1995) and does not contradict a Late Pliocene/Pleistocene regime for the main currents, which would be substantially comparable to the modern one.

The results of a detailed analysis of endemic fossil mollusks (Table 4) show a slight increase in gastropods from the Pliocene to the Pleistocene (the ages of the fossiliferous deposits are based on original research or subsequent age redeterminations), whereas bivalves display substantially equal numbers. Because evidence to support a huge colonization of the Galápagos during the Holocene does not exist, the marked difference between Pleistocene (33 taxa) and modern (123 taxa) endemic gastropods (with regard to bivalves, the dissimilarity is less significant) is probably due to biases in the fossil record (limited sample sizes, patchy distributions, etc.).

Taking into account fossil mollusks at generic and specific ranks together, gastropods largely outnumber bivalves in both Panamic and endemic components, and the modern assemblage shows a similar pattern. Kay (1991) compares the Galápagos and mainland mollusk assemblages on the basis of the selectivity index of Vermeij (1987), which appears higher for bivalves than for gastropods. This evidence might explain the predominance of gastropods over bivalves in the fossil faunas too, even though the ratio varies, sometimes markedly, among the fossil assemblages (Table 4). In the Isabela assemblage, the ratio is even slightly favorable to bivalves. It is difficult to establish whether these differences reflect different taphonomic histories, biases linked to sampling, different paleoenvironments (intertidal or subtidal, soft or hard bottom, etc.), or different responses in ranging trophic and other ecologic variables. Probably, different factors are (and were) operative in assembling the characteristics of the mollusk faunas of the archipelago. However, according to Kay (1967), the main factor is the substrate: the high ratio of gastropods to bivalves and the percentage of epifaunal versus infaunal bivalves compared with what occurs in the mainland faunas is due to the lack of broad sandy/silty sea bottoms that are typical of continental offshore areas. Therefore, relevant immigrations do not necessarily mean relevant colonizations. Many larvae arriving from different directions as a result of successful dispersals are not able to colonize new habitats because of the absence of favorable conditions.

In conclusion, comparisons among fossil and modern molluscan faunas in the Galápagos Islands indicate a similar biogeographic pattern of a Panamic component outnumbering the endemic one and negligible values for other groups. This model essentially reflects the proximity of the Central and South American shores, the regime of the main oceanic currents in the tropical/subtropical eastern Pacific, and the presence of physical barriers. With regard to the taxonomic composition, most of the fossil assemblages and the modern one show gastropods markedly predominant over bivalves, among which epifaunal elements are well represented. Different factors may contribute to explain

this evidence, but the main role is probably played by the marine substrate of these oceanic islands.

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References

Bernard, F.R., 1983. Catalogue of the living bivalvia of the eastern Pacific ocean: Bering Strait to Cape Horn. Canadian Special Publication of Fisheries Aquat. Sciences 61, 102 pp.

Bianucci, G., Cantalamessa, G., Landini, W., Ragaini, L., Valleri, G., 1993. Coarse grained deposits of Cerro Colorado, Isla Santa Cruz, Galápagos archipelago (Ecuador). Documents de Laboratoire de Géologie de Lyon 125, 59–71.

Bianucci, G., Cantalamessa, G., Landini, W., Ragaiani, L., Valleri, G., 1997a. Fossil mollusk association from Isabela Island (Galápagos Ecuador). Bollettino della Società Paleontologica Italiana 36 (1–2), 277–281.

Bianucci, G., Cantalamessa, G., Landini, W., Ragaiani, L., Valleri, G., 1997b. Paleontologic and sedimentologic observations on the Canoa Formation (Manabì Basin Ecuador). Bollettino della Società Paleontologica Italiana 36 (1–2), 85–96.

Bratcher, T., Burch, R.D., 1971. The Terebridae (Gastropoda) of Clarion, Socorro, Cocos and Galápagos islands. Proceedings of the California Academy of Sciences 37 (21), 537–566.

Coan, E.V., 1988. Some bivalve records from the Galápagos Islands. Annual Report of the Western Society of Malacologists 21, 11–12.

Coan, E.V., 1999. The eastern Pacific Sportellidae (Bivalvia). The Veliger 42 (2), 132–151.

Collins, L.S., Budd, A.F., Coates, A.G., 1996. Earliest evolution associated with closure of the tropical American seaway. Proceedings of National Academy of Sciences 93, 6069–6072.

Cronin, T.M., Dowsett, H.J., 1996. Graphic correlation of marine deposits from the Central American Isthmus: Implications for late Neogene paleoceanography. In: Jackson, J.B., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America, University of Chicago Press, Chicago, pp. 57–75.

Dall, W.H., 1924. Note on fossiliferous strata on Galápagos Islands explored by W.H. Ochsner of the expedition of the California Academy of Sciences 1905–6. Geological Magazine 61, 428–429.

Dall, W.H., Ochsner, W.H., 1928. Tertiary and Pleistocene mollusks from the Galápagos Islands. Proceedings of California Academy of Sciences 17 (4), 89–139.

Di Geronimo, I., Robba, E., 1976. Metodologie qualitative e quantitative per lo studio delle biocenosi e delle paleocomunità marine bentoniche. C.N.R. Gruppo Paleobenthos, Rapporto di lavoro 1, 1–35.

Di Geronimo, I., Li Gioi, R., Sciacca, V., 1982. La fauna pleistocenica dell'abbeveratoio Conzo (Grammichele, Catania). Geologica Romana 21, 577–601.

Duque-Caro, H., 1990. Neogene stratigraphy, paleoceanography and paleobiogeography in northwest South America and the evolution of the Panama seaway. Palaeogeography Palaeoclimatology Palaeoecology 77, 203–234.

Finet, Y., 1991. The marine mollusks of the Galápagos Islands. In: James, M.J., (Ed.), Galápagos Marine Invertebrates, Plenum Press, New York, pp. 253–280.

Finet, Y., 1994a. Marine molluscs of the Galápagos. Gastropods. A monograph and revision of the families: Haliotidae, Scissurellidae, Fissurellidae and Lottiidae. Monographs on Galápagos Mollusca 1. L'Informatore Piceno, Ancona.

Finet, Y., 1994b. The marine mollusks of the Galápagos Islands: a documented faunal list. Muséum d'Histoire Naturelle de Genève, Genève.

Finet, Y., 1995. Marine molluscs of the Galápagos. A monograph and revision of the families: Trochidae, Skenetidae, Turbinidae and Neritidae. Monographs on Galápagos Mollusca 2. L'Informatore Piceno, Ancona.

Garcia-Talavera, F., 1993. Resultados científicos del Proyecto Galápagos: patrimonio de la Humanidad. No. 3. Los Moluscos Marinos Fósiles. Resultados Cientificos del Proyecto Galápagos TFMC 3, 5–61.

Glynn, P.W., Wellington, G.M., 1983. Corals and Coral Reefs of the Galápagos Islands, University of California Press, Berkeley.

Grig, R.V., Hey, R., 1992. Paleoceanography of the Tropical Eastern Pacific Ocean. Science 255, 172–178.

Haug, G.H., Tiedemann, R., 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermoaline circulation. Nature 393, 673–676.

Hertlein, L.G., 1972. Pliocene fossils from Baltra (South Seymour) Island, Galápagos Islands. Proceedings of the California Academy of Sciences 39 (3), 25–46.

Hertlein, L.G., Strong, A.M., 1939. Marine Pleistocene mollusks from the Galápagos Islands. Proceedings of the California Academy of Sciences 32 (24), 367–380.

Hickman, C.S., Lipps, J.H., 1985. Geologic youth of Galápagos Islands confirmed by marine stratigraphy and paleontology. Science 227, 1578–1580.

James, M.J., Pitt, W.D., 1984. Biogeographic affinities of Pleistocene and recent Galápagos marine mollusks. Annual Report of the Western Society of Malacologists 20, 28.

Kaiser, K.L., 1997. The recent Molluscan fauna of the islas Galápagos. The Festivus 29, 67 (Suppl.).

Kay, E.A., 1967. The composition and relationships of the marine molluscan fauna of the Hawaiian Islands. Venus 25, 94–104.

Kay, E.A., 1991. The marine mollusks of the Galápagos. In: James, M.J., (Ed.), Determinants of insular marine fauna, Galápagos Marine Invertebrates, Plenum Press, New York, pp. 235–252.

Keen, A.M., 1971. Sea shells of Tropical West America, Stanford University Press, Stanford.

Lipps, J.H., Hickman, C.S., 1982. Paleontology and geologic history of the Galápagos Islands. Geological Society of America, Abstracts with Programs 14 (7), 548.

Malmquist, D.L., 1991. The past as a key to the present taphonomy and paleoecology of the Urvina Bay uplift. In: James, M.J., (Ed.), Galápagos Marine Invertebrates, Plenum Press, New York, pp. 393–421.

Nesbitt, E.C., Pitt, W., 1986. Nassarius (Gastropoda: Neogastropoda) from the Galápagos Islands. The Veliger 28 (3), 294–301.

Olsson, A.A., 1961. Mollusks of the Tropical Pacific, Paleontological Research Institute, Ithaca, NY.

Pavia, G., Chiambretto, L., Oreggia, G., 1989. Paleocomunità a molluschi nel Pliocene inferiore di Breolungi (Mondovì, Italia NW), 3° Simp. Ecol. Paleoecol. Com. Bent., Taormina, Atti, pp. 521–569.

Piazza, M., Robba, E., 1994. Pectinids and oysters from Pliocene Loreto Basin (Baja California Sur, Mexico). Rivista Italiana di Paleontologia e Stratigrafia 100 (1), 33–70.

Piazza, M., Robba, E., 1998. Autochtonous biofacies in the Pliocene Loreto

Basin, Baja California Sur, Mexico. Rivista Italiana di Paleontologia e Stratigrafia 104 (2), 227–262.

Pilsbry, H.A., Olsson, A.A., 1941. A Pliocene fauna from Western Ecuador. Proceedings of the Academy of Natural Sciences of Philadelphia 93, 1–79.

Pitt, W.D., James, M.J., 1983. Late Cenozoic marine invertebrate paleontology of the Galápagos Islands. Annual Report of the Western Society of Malacologists 15, 14–15.

Pitt, W.D., James, M.J., Hickman, C.S., Lipps, J.H., Pitt, L.J., 1986. Late Cenozoic marine mollusks from tuff cones in the Galápagos Islands. Proceedings of the California Academy of Sciences 44 (12), 269–282.

Ragaini, L., Mariani, R., 1992. Analisi paleoecologica della malacofauna pliocenica di Camino Tondo (Grosseto, Italia). Atti Società toscana Scienze Naturali, Memorie serie A 99, 1–27.

Sanders, H.L., 1958. Benthic studies in Buzzards bay. I. Animal-sediment relationships. Limnology and Oceanography 3, 245–258.

Taviani, M., 1979. I molluschi marini raccolti dalla spedizione 'L.Mares-G.R.S.T.S.' alle Isole Galápagos. 1. Gastropoda e Bivalvia. Museo Zool. Firenze Edit., Firenze, 339–399.

Vermeij, G.J., 1987. The dispersal barrier in the tropical pacific: implications for molluscan speciation and extinction. Evolution 41 (5), 1046–1058.

Walker, S.E., 1991. Taphonomy and paleoecology of Villamil fossil Megagastropods of Isla Isabela. In: James, M.J., (Ed.), Galápagos Marine Invertebrates, Plenum Press, New York, pp. 423–437.

Walker, S.E., 1995. Taphonomy of modern and fossil intertidal gastropod associations from Isla Santa Cruz and Isla Santa Fe, Galápagos Islands. Lethaia 28, 371–382.

Wellington, G.M., 1984. Marine environment and protection. In: Perry, R., (Ed.), Galápagos, Pergamon Press, Oxford, pp. 247–263.

Wolf, T., 1895. Die Galápagos-Inseln. Verhandlungen der Gesellschaft Erdkunde zu Berlin 22, 246–265.